Procolpochelys grandaeva (Leidy), An Early Carettine Sea Turtle

RAINER ZANGERL
Curator of Fossil Reptiles

AND

WILLIAM D. TURNBULL
Preparator, Department of Geology

INTRODUCTION

Knowledge of fossil sea turtles has shed some light on the evolution of the Recent genera, but our information is still meager. As a consequence, the relationships among the four living species have been interpreted in different ways. One of the few fossil sea turtles that seem to have closer phylogenetic ties to the Recent loggerheads and ridlies (Carettini; see Zangerl, in press) is *Procolpochelys grandaeva* (Leidy), a form that has hitherto been known only from fragments.

The first mention of this turtle was made by Leidy (1851) under the name of *Chelonia grandaeva;* the type specimen consists of three neural plates, first stated to have come from the Green Sand of New Jersey, but later (Leidy, 1856) from the Miocene Marl of Salem County, New Jersey. The latter age and locality are apparently correct. In 1856, Leidy described some additional fragmentary material. Still more fragmentary material was described by Cope (1870); he illustrated only the right scapula and the proximal end of a humerus (described as femur, p. 154, and labeled as humerus, p. 251). The description (pp. 153–154) is under the name of *Chelone grandaeva,* but in the same volume (p. 235) Cope erected the genus *Puppigerus* for eight of the London Clay species and included *Chelone grandaeva* in the new genus. Lydekker (1889) made *Chelone longiceps* the type of the genus *Puppigerus.* Since the latter species is not congeneric with *Chelonia grandaeva,* Hay proposed a new

name, *Procolpochelys*, for the present turtle. Hay (1908) reviewed the previously described specimens and found further material in the paleontological collections at Rutgers College, New Brunswick, New Jersey, and at Princeton University. All of this material consisted of fragments, by far the greater number of which were found in the collections of Princeton University. Hay studied this lot of broken plates and concluded that there were "at least four turtles, belonging apparently to two genera" represented. He states: "It has been found impracticable to separate these satisfactorily, but apparently there are parts of three individuals of the present species." Nevertheless, Hay described such parts as were readily identifiable and rendered a rather modest illustration of a few of the peripheral bones.

Some time ago, the senior author had the opportunity of visiting the Princeton University collection and saw the large tray of fragments mentioned by Hay. From past experience it seemed probable that these fractured plates would yield to patient and competent "piece-fitting," and the material was thus borrowed for further preparatorial scrutiny.

The fragments of three specimens were so intermingled that the task of fitting the broken pieces together proved difficult and time-consuming, but the results are highly satisfactory.

While the three specimens bear the Princeton University numbers PU 16333, PU 16334, and PU 16335, there are some elements that cannot be definitely assigned to a specific individual and these were thus arbitrarily numbered with one of the specimens.

We wish to thank Dr. Glenn L. Jepsen of Princeton University for the loan of this interesting material. Miss Maidi Wiebe of Chicago Natural History Museum prepared the illustrations.

DESCRIPTION OF THE MATERIAL

The material after preparation.—The Princeton material of *Procolpochelys grandaeva* now consists of four restored partial carapaces, belonging, very probably, to three individuals; these will be referred to by the catalogue numbers PU 16333, PU 16334, and PU 16335 in the following description (figs. 77–80). Individual PU 16333 is notably smaller than the other two. Specimen PU 16334 consists of two restored portions, which, while they do not contact, are here presumed to have been from the same individual (they are in complete accordance in size and degree of ossification, and there is no duplication of parts; positive proof is, of course, impossible). Speci-

mens PU 16334 and PU 16335 are of nearly the same size, though the latter was the largest and probably the oldest individual of the three. There are nineteen peripherals, one of them suturally attached to the carapace disc of PU 16334. The other peripheral bones can be assigned to the three specimens as follows: Right and left pairs of peripherals 2 and 3 (fig. 82) are too small for PU 16334 and thus probably belong to PU 16333. Contiguous right peripherals 6 through 10 and left peripherals 9 through 11 (fig. 83) are quite certainly too large for PU 16333 and probably belong to PU 16335. Of the remaining six elements, two are identifiable as left peripherals 10 and 11, and two others (apparently belonging to the same specimen) as right peripherals 11 and 12 (fig. 82). These elements, which include a supernumerary twelfth peripheral, probably belong to PU 16334, in which the posterior shell area contains paired supernumerary ninth costal plates (fig. 78). There remain two peripherals, one probably a left fifth (fig. 82) that may belong to PU 16333, the other a partial left first, quite certainly belonging to specimen PU 16335. The incomplete pygal plate (fig. 83) probably belongs to PU 16334.

Unfortunately, the remains of the plastra are rather meager and belong to at least two individuals, probably PU 16333 and PU 16335, although, as was pointed out in the case of the carapacial parts of PU 16334, it is impossible to prove this beyond all doubt. The postero-medial portion of the hypoplastra, the xiphiplastra, most of the hyoplastra, the entoplastron, and the anterior ends of the epiplastra are entirely unknown. The preserved parts can be identified as shown in the reconstructions (figs. 90, 91).

Among the known portions of the plastron, there is an incomplete left hypoplastron, which is adequate to provide a width measurement. A fragment best interpreted as part of the medial portion of the right hyoplastron is also present (fig. 84). Both could belong to individuals PU 16334 or PU 16335, judging by their size, shape, and age as indicated by the lateral and medial sutural growth of the plates. Another fragment of the lateral portions of the left hyo- and hypoplastron (fig. 84) can reasonably be assigned to PU 16333 on the same criteria. Two epiplastral pieces (fig. 84) may belong to PU 16333, PU 16334, or PU 16335.

The general form of Procolpochelys.—The carapace of *Procolpochelys* (figs. 87–89) is thick, elongated, and relatively slender, much as in the genus *Caretta* (fig. 92). However, the anterior rim of the nuchal plate is but very slightly excavated above the neck,

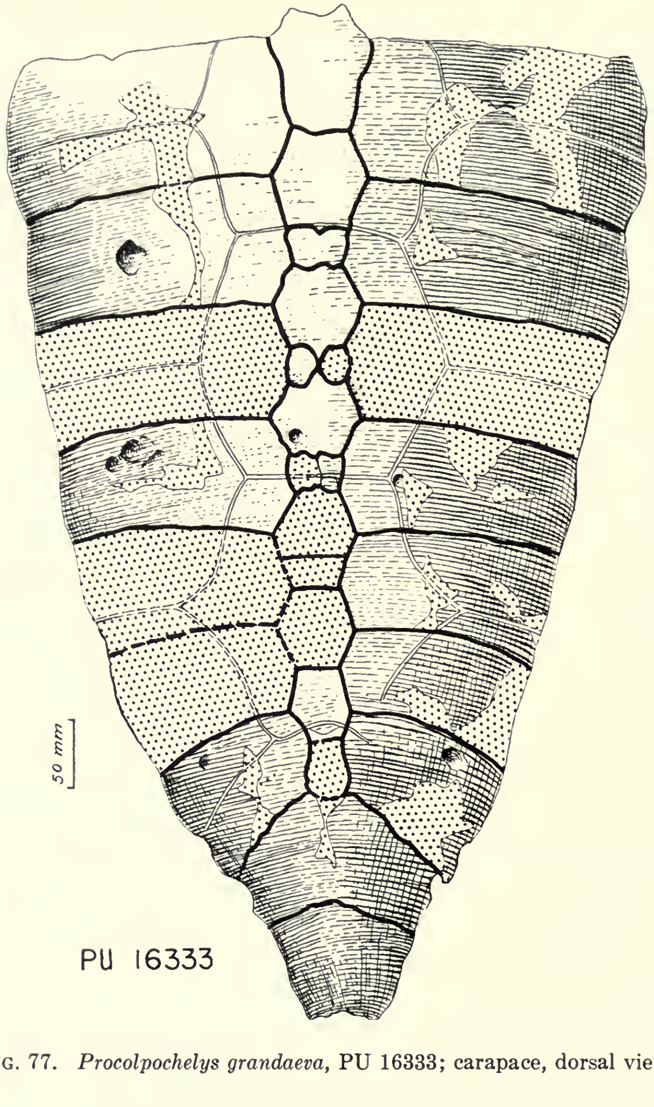


FIG. 77. *Procolpochelys grandaeva*, PU 16333; carapace, dorsal view.

and the peripherals do not indicate the position of the limbs in the outline of the carapace. There is no evidence that the present specimens are juveniles, yet in all of them there is a continuous costo-peripheral fontanelle, from the second costal plate to the suprapygal area. This would indicate that *Procolpochelys* was more pelagic in its habits than either of the living Carettini.

In the accompanying figures illustrating various parts of the specimens, the scale is included for convenience in taking measurements. In taking measurements from these figures caution must be used because of the foreshortening incorporated in reducing three dimensions to two and because of the crushing and other deformations of the bones. For this latter reason, it was felt that an extensive tabulation of measurements was of little use. Below is a single comparable measurement from each of the three specimens as a measure of relative size.

Width of second costal plate along curve of suture with third costal	Left cm.	Right cm.
Specimen PU 16333	21.0	21.0
Specimen PU 16334	ca. 25.0 (23.0 preserved)	24.0
Specimen PU 16335	27.0	26.0

Carapace.—In the smallest individual, PU 16333, the carapace is essentially known from the second pair of costal plates to the lower suprapygal (fig. 77). About the same area is preserved in specimen PU 16335 (fig. 80) except for the neural bones and the lower suprapygal. Specimen PU 16334 shows the anterior and posterior areas of the carapacial disc (fig. 78).

The most significant feature of the carapace of this form is the neural series, as was realized by Leidy (1851), the original describer of the species. Two of the neural plates that were available to Leidy (figured by Hay, 1908, p. 216) are flat, hexagonal elements, about as wide as long, and each has a medial, tooth-like sutural process. Hay considered these processes to be on the posterior edge of the plates and concluded that "some of the neurals were sharply notched in front." The neural series of PU 16333 shows the significance of the medial processes on the neurals. Here in two large, adjoining neurals these processes may face one another, separating a smaller element between them into right and left ossicles (fig. 77). The neural series of *Procolpochelys*, as seen from the neural bones, or from the outlines of the neuro-costal sutures (where the neurals themselves are missing), consists of transversely and sometimes even longitudinally subdivided plates, essentially as in the Recent genus *Lepidochelys* (see Deraniyagala, 1939, p. 149, fig. 60). Although this subdivision of the neural bones is subject to considerable individual variation in both *Lepidochelys* and *Procolpochelys*, it does not seem to be entirely irregular. Neurals of

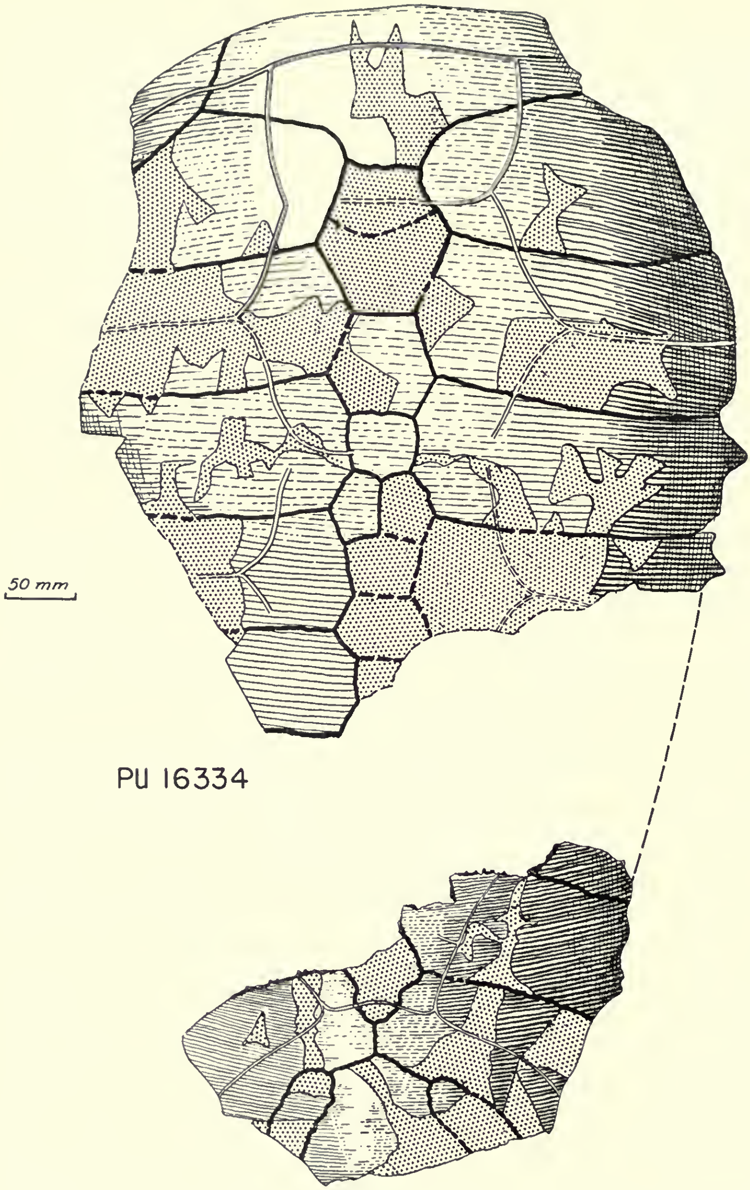


FIG. 78. *Procolpochelys grandaeva*, PU 16334. Two partial carapacial discs that probably belong to the same individual; dorsal view.

the common pattern of elongated, dorsally smooth and flat, hexagonal shape with short antero-lateral and long postero-lateral sides may be divided transversely either at mid-length or in the posterior half into two elements, *a* and *b* (figs. 77, 78). Furthermore, in *Procolpochelys* either the anterior or the posterior portion may be

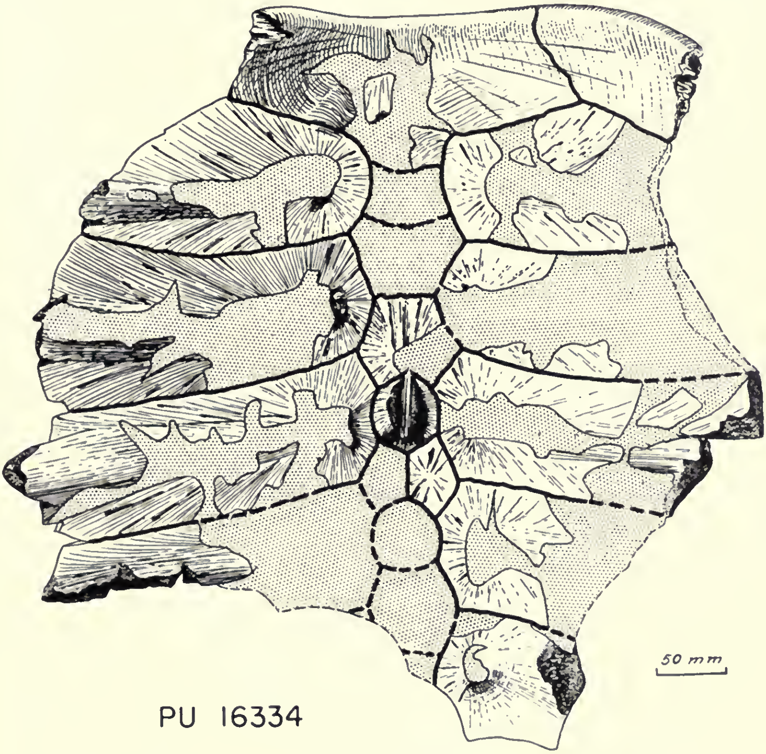


FIG. 79. *Procolpochelys grandaeva*, PU 16334; anterior portion of carapace, ventral view.

longitudinally divided, so that the area occupied by one neural in other genera may be filled by two or three suturally united plates in *Procolpochelys* (figs. 77, 78).

In specimen PU 16333 the anteriormost neural is number 2 in the series. It is normally elongated and hexagonal and protrudes a short distance forward beyond the second pair of costal plates. The third neural in this individual is transversely divided at the level of the posterior furrow of the second vertebral shield (fig. 77).

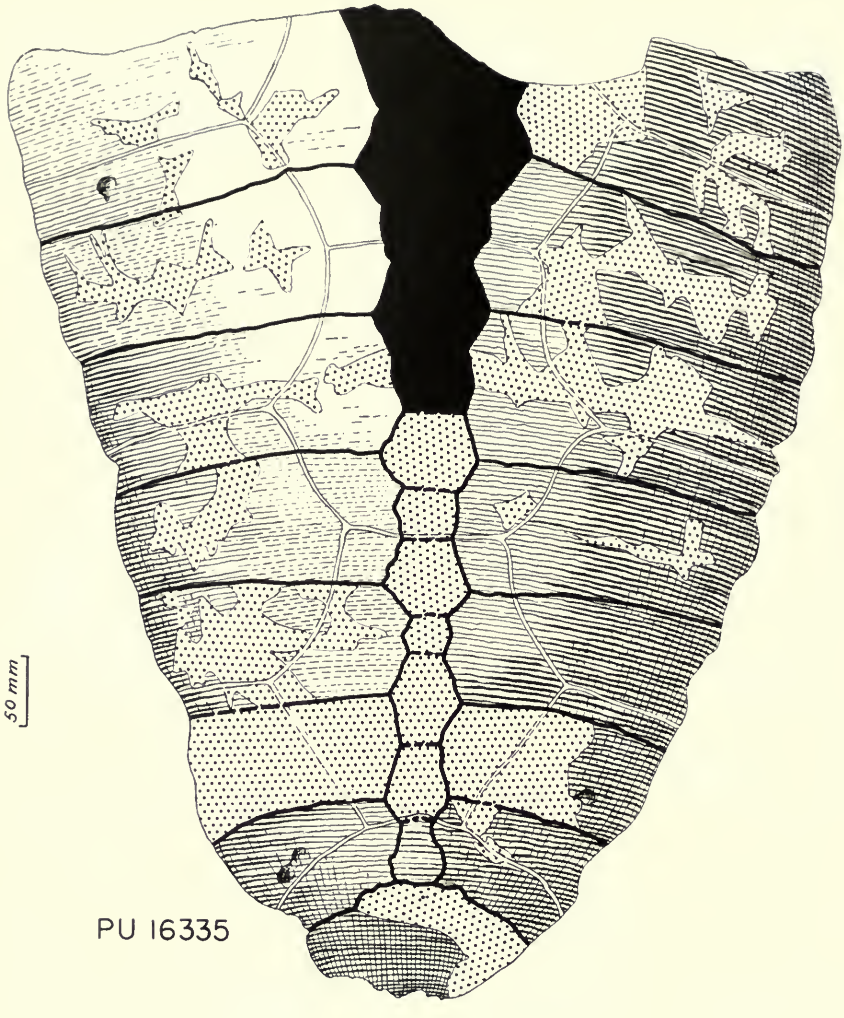


FIG. 80. *Procolpochelys grandaeva*, PU 16335; carapace, dorsal view.

The larger portion, neural 3a, is almost a regular hexagon, whereas 3b is an irregularly quadrangular piece. Dorsally, the posterior suture of 3a forms a short, median projection backward into 3b; ventrally, this condition is reversed. Neurals 4 and 5 of this specimen are similarly divided, but in neural 4 the ossicle 4b is longitudinally divided into two small plates by a posterior tooth-like process of 4a and a similar anterior projection of neural 5a. Neural element 5b is not entirely preserved; it may or may not have been

longitudinally divided. The posterior furrow of the third vertebral shield extends over this plate (fig. 77). Neurals 6 and 7 are missing. Dorsally the adjoining costal plates appear to indicate that they were undivided, more or less regularly hexagonal bones. Ventrally, however, neural 6 can be seen to be transversely divided (6a and 6b). The eighth neural is irregular in shape. Its antero-lateral sides are about equal to the postero-lateral sides. The posterior imprint of the fourth vertebral shield runs across this plate posteriorly. There was a ninth neural of suboval outline.

It may be noted that the proximal suture edges of the costal plates in turtles with a normal neural series (e.g. *Chelonia*) form two facets. In *Procolpochelys* they are three-faceted, because of the transverse division of the neurals (figs. 77, 78, and 80).

The formulae of the neural elements in the three specimens of *Procolpochelys* may be compared as follows:

individual	N 1	N 2	N 3	N 4	N 5	N 6	N 7	N 8	N 9
PU 16333	? S probably small	S	a – b	a – bb	a – b	a – b	S	S	S
PU 16334	S small	S	a – b	aa – b	a – b	?	?	S*	S*
PU 16335	? S probably small	S	a – b	a – b	a – b	a – b	? S	? S	S

S = single

a–b = NEURAL TRANSVERSALLY DIVIDED INTO COMPONENTS a – b

aa bb = parts of neurals longitudinally divided

* = alternative interpretation: Neural 8a — b, N9 absent

FIG. 81. Pattern of fragmentation of neural plates in the three individuals of *Procolpochelys grandaeva*.

In specimen PU 16334 the first neural appears to have been small. The second neural is undivided, as in individual PU 16333, and is noticeably wider than any of the following neurals. The third neural is divided transversely into two portions, 3a and 3b. The shield furrow of the second vertebral element runs across 3b at mid-length (fig. 78). The fourth neural is subdivided into at least three parts, as follows: 4a, right; 4a, left; and 4b. Here it is the anterior portion that became longitudinally divided. The fifth

neural again is divided into 5a and 5b (fig. 78). In the posterior area of the shell of PU 16334 there is a vacancy for two neural ossicles that can be interpreted either as neural 8a and 8b, or as neurals 8 and 9. The second of these plates does not reach the upper suprapygal (fig. 78).

In PU 16335 neural 9 is the only one preserved. Anterior to this, the outlines formed by the sutures of neural and costal plates reveal most of the neural pattern as follows: N2, N3a and b, N4a and b, N5a and b, N6a and b, N7, N8, and N9. Of course, there is no evidence preserved to indicate that any were longitudinally split. The posterior furrow of the second vertebral shield crossed N3b, that of the third vertebral shield N5b near its suture with N6a; the posterior furrow of the fourth vertebral shield crossed the neural series at N8 near the junction with N9 (fig. 80).

The costal plates in all three individuals are somewhat flattened by formation pressure; in the largest specimen this is responsible for the distortion in the anterior part of the mount (fig. 80). The costals are quite thick, up to 20 mm. along the sutures in the anterior part of the carapace and about 8 mm. in the posterior area. Laterally the costals end abruptly, thus sharply outlining the inner boundaries of the costo-peripheral fontanelles. On the dorsal side, the plates are smooth and the shield furrows are not very deeply imprinted. The normal number of costal plates, as in most turtles, is eight. Specimen PU 16334 has nine pairs (fig. 78), an individual variation rather frequently observed in some turtle families (see Zangerl, 1953, p. 190).

The nuchal plate (PU 16334) is bluntly rounded in front, and scarcely excavated above the neck. Most of the surface bone near the midline on the ventral side is missing, but there remains at least a small part of the ventral boss with which the neurapophysis of the eighth cervical vertebra articulates.

There are two suprapygal elements in about the same arrangement as in *Lepidochelys,* but these plates are reduced laterally by the backward extension of the costo-peripheral fontanelles (fig. 77).

Only one partial pygal plate (fig. 83) is available. It is approximately square in outline and does not form a notch at the back end of the carapace.

The peripheral bones (figs. 82, 83) are of about equal width anteriorly and posteriorly. The normal number of peripheral plates was unquestionably eleven on a side. The posterior peripherals, interpreted as belonging to PU 16334 (fig. 82), indicate that there

were twelve elements in this individual, a variation fairly frequently observed and not surprising in an individual with an extra pair of costal plates. The bridge peripherals (numbers 4 to 7) differ from those of Recent cheloniids in having a well-developed ventral leaf; they are V-shaped in cross section, with the ventral limb of the V

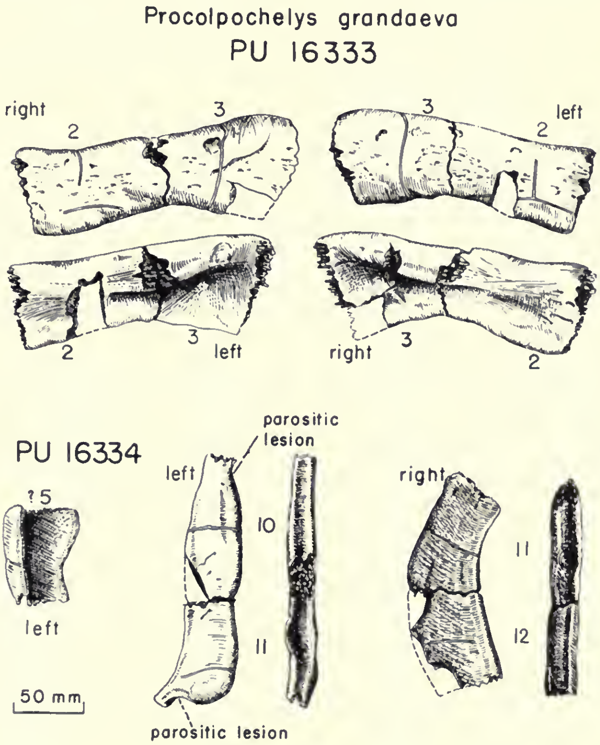


FIG. 82. *Procolpochelys grandaeva.* Top: right and left, anterior peripherals of specimen PU 16333 in dorsal and ventral views. Bottom left: ?fifth peripheral of specimen PU 16334 in ventral view. Bottom center: left tenth and eleventh peripherals of specimen PU 16334 in ventral and medial views. Bottom right: right eleventh and twelfth peripherals of specimen PU 16334 in ventral and medial views.

only slightly shorter than the dorsal limb. The dorsal surface of the peripherals is slightly concave, the ventral surface convex. Peripherals 10 and 11 of the left side of PU 16334 (fig. 82) are of peculiar outline because of severe parasitic lesions or other kind of injury. The two pairs of peripherals, numbers 2 and 3 (fig. 82), are of exactly the same stage of ossification and are too small to

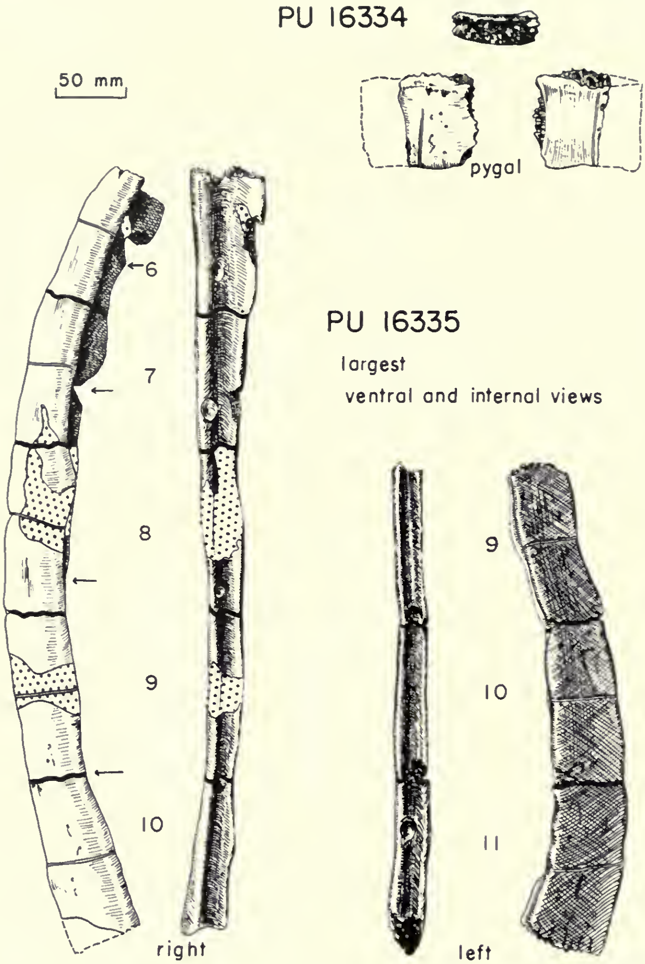


FIG. 83. *Procolpochelys grandaeva.* Top right: pygal plate of specimen PU 16334 in dorsal, ventral, and anterior views. Left: right peripherals 6 to 10 in ventral and medial views, specimen PU 16335. Bottom right: left peripherals 9 to 11 of the same specimen, ventral and medial views.

fit PU 16334; very probably they belong to specimen PU 16333. However, they differ notably in length as shown below:

	Length at midline mm.
P2 left	ca. 95
P2 right	ca. 100
P3 left	ca. 80
P3 right	ca. 90

A pit for the reception of the rib end of the first costal plate enters the ventral side of the third peripheral (figs. 82, 87). The inner edges of these peripherals were not suturally connected with the first costal plates, but faced fontanelles. In PU 16334 the right first costal plate shows a distal suture edge a short distance beyond the contact with the first peripheral; at least part of this second peripheral must have been suturally attached to the costal plate (figs. 88, 89).

The shield pattern of the carapace can be determined satisfactorily (figs. 87–89). It consists of five vertebral, four pairs of pleural, and twelve pairs of marginal scutes (thirteen in PU 16334). The lateral extent of the cervical scute is not known. The vertebral shields are only slightly wider than long.

Plastron.—In its general proportions, the plastron of *Procolpochelys* agrees reasonably well with that of *Caretta*, perhaps being somewhat stouter, more massive and chunky than the latter. The left hypoplastron belonging to specimen PU 16335 (fig. 84) is adequate to give two rough measurements. The first of these is the length of the plate at its shortest dimension, from the inguinal notch to the suture with the hyoplastron (between 12.0 and 12.5 cm.). The other measurement is the width of the hypoplastral plate, which gives an indication of the total plastral width. Along the suture, this measures 21.0 cm. The measurement from the tips of the lateral digitations to the medial fontanelle is 30 cm. The medial digitations are missing, but from the reconstruction based on the carapace width, it is reasonable to assume that the total plastral width was about 70 cm.

The epiplastral fragments that are preserved—both are posterior halves—are remarkable in that they have an extreme, almost suture-like rugosity on their antero-lateral edges (fig. 84).

The postero-medial fragment of a right hyoplastron is considered as probably having belonged to individual PU 16335. It bears a

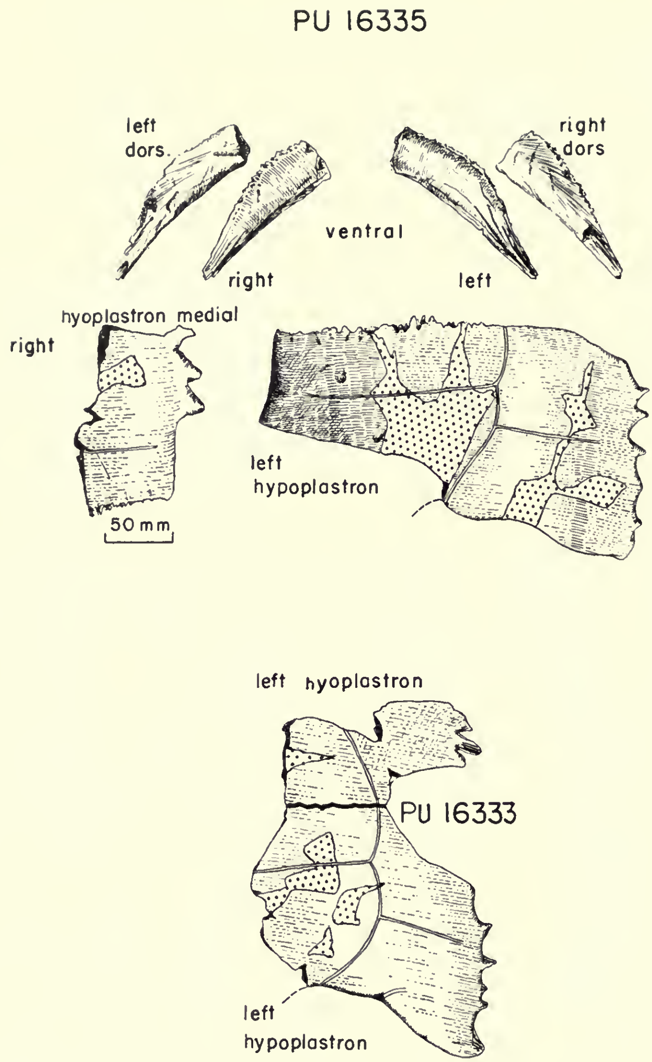


FIG. 84. *Procolpochelys grandaeva.* Top: right and left epiplastral fragments probably belonging to specimen PU 16335, dorsal and ventral views. Middle left: ventral view of right hyoplastral fragment probably belonging to specimen PU 16335. Middle right: ventral view of left hypoplastron of the same specimen. Bottom: ventral view of left hyo- and hypoplastral fragments of specimen PU 16333.

shield furrow that runs nearly parallel to the hyo-hypoplastral suture about 4 cm. anteriorly. The postero-lateral hyoplastral fragment (PU 16333) suturally joins with the lateral half of a hypoplastral plate. It also bears a sulcus that runs in an arc forward and mediad, very near the lateral fontanelle. There is no indication of a junction with that sulcus, which in the other fragment paralleled the hyo-hypoplastral suture. Since most sulci are clearly visible, it is assumed either to have been anterior to the broken edge of the fragment or possibly to have run along the break as indicated in figure 90.

The half hypoplastron that joins with the above hyoplastral fragment bears a number of shield furrows (figs. 84, 90). The furrow running from the hyoplastron continues its arc for about 3.5 cm. onto the hypoplastron, where there is a junction with the furrow that proceeds mediad and roughly parallel to the hyo-hypoplastral suture. This is the anterior boundary of the femoral shield. The antero-posterior sulcus proceeds from this junction in a more closely curved course to the deepest point of the inguinal notch. About midway between junction and notch, a sulcus runs laterally (figs. 84, 90). This is probably the anterior boundary of the last inframarginal shield.

There would seem to be a notable difference in plastral sulcus pattern between *Procolpochelys* and average specimens of *Caretta,* where the anterior boundary of the last inframarginal shield intersects the lateral furrow of the abdominal shield rather than that of the femoral shield.

From the shape of the edges of the fontanelles and the correlated extent of hyo-hypoplastral suture growth, we judge that these suturally joined fragments belong to specimen PU 16333.

The large, nearly complete hypoplastron (fig. 84) is thought to belong to specimen PU 16335 for the same reasons. The fontanelles have been considerably encroached upon and the lateral edge of the inguinal notch has developed a protuberance that modifies the curve of the notch (figs. 84, 91). This is faintly suggested in the younger individual. The sulci agree well with those of the younger specimen. Between the two individuals, the following five scutes may be identified: ?pectoral (in PU 16335), abdominal, femoral, and the two posterior inframarginals. The more anterior of the two inframarginals is large and we presume that a furrow may have run across the lateral fontanelle at the hyo-hypoplastral suture. In specimen PU 16333, lateral to the faint posterior extension on the

smooth curve of the inguinal notch, there is a trace of another sulcus that probably delimits the inguinal shield.

Vertebrae.—Associated with these specimens are a few vertebrae. Of the cervical series, there is only one fragment of an eighth cervical neurapophysis (pl. 4). It presents the characteristic postzygapophysis with its dorsal contact surface for the articulation with the ventral boss on the nuchal plate. When compared with the corresponding parts in *Chelonia mydas* and *Caretta caretta* (pl. 4), it shows peculiarities of both. The posterior outline of this nuchal process is straight in *Chelonia* but V-shaped in *Caretta* and *Procolpochelys* (pl. 4). On the other hand, the nuchal process has a lateral crest that runs forward in *Chelonia* and *Procolpochelys* but not in *Caretta* (pl. 4).

In general appearance the few remains of shell vertebrae are quite similar to those of *Caretta caretta.* Their mode of attachment to the neural plates is of some interest, because it may differ from the conditions in *Caretta* and *Lepidochelys.* Direct point for point comparison with these latter forms, however, is not possible at present, since that would involve dissecting the skeletons. Some neurapophyses of *Procolpochelys* are co-ossified with the neural plates; others are merely attached to their under sides by means of foot-like enlargements of the spinal processes. In the latter case, corresponding attachment scars are seen on the ventral sides of the neurals. This condition is notable only in the anterior portion of the shell, back to neural 3a (see fig. 85). Neurals 3b (in specimens PU 16333 and PU 16334), 4b, and 5b (in PU 16333) were fused to spinal processes. The intervening neural elements show sagittal ridges that supported the anterior and posterior extensions of the neurapophyses, but were not co-ossified with them.

In *Chelonia, Eretmochelys,* and *Caretta* (with unfragmented neural series), the first and second shell vertebrae are attached to the first neural plate; the neurapophysis of the first vertebra is usually not co-ossified with the neural plate (if a preneural element is developed, the spinal process of the first vertebra may be fused with it). The third vertebra is fused to the under side of neural 2, the fourth to neural 3, etc. In all of these forms, the neurapophyses (except for the first one) are thus fused to the neural plates above them, especially to the posterior portions of them. With the fragmentation of the neural pattern in *Procolpochelys,* the attachments of the neurapophyses remain in the same relative places as in the nonfragmented forms, namely, on neurals 3b, 4b, 5b, etc. (fig. 85).

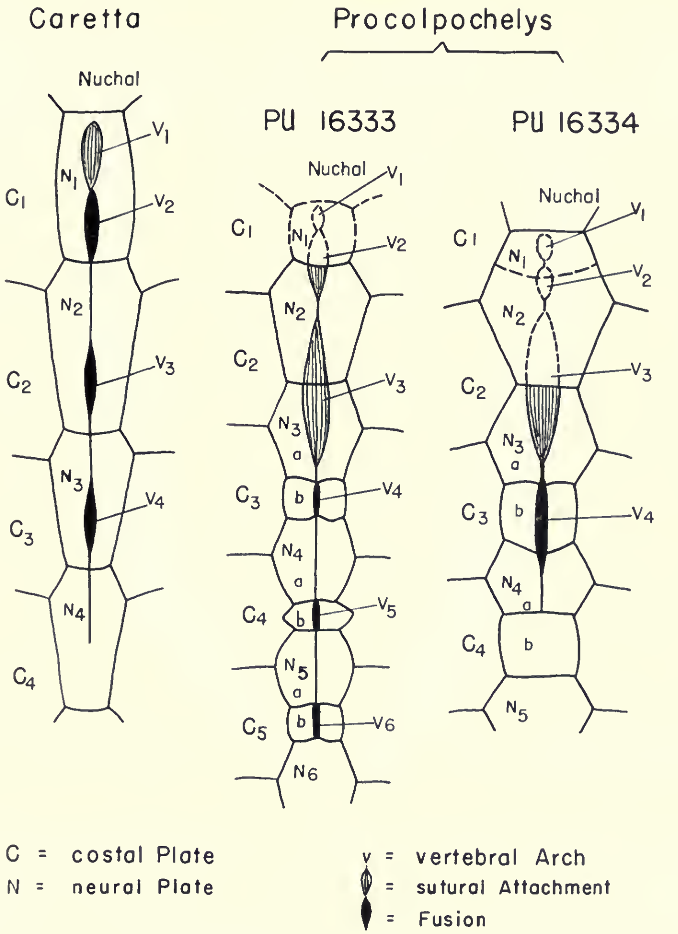


FIG. 85. Semidiagrammatic representation of the attachments of the neural arches to the neural plates in the anterior portion of the carapace in *Caretta* and *Procolpochelys*.

Anterior to neural 3b, the spinal processes are not co-ossified with the neural plates but are merely attached to them by connective tissue along suture-like contact rugosities. The significance of this is not understood; it is subject to different interpretations. In *Lepidochelys,* where the neural series is fragmented much as in *Procolpochelys,* the spinal processes of the anterior three shell vertebrae are likewise not co-ossified with the neurals above them. In both forms, the spinal processes in question are located at the junctions of two adjoining neural elements. It is difficult to understand why

they should not co-ossify with both elements, unless there is a certain amount of movability of the vertebrae. One might also think of the influence that neighboring structures may exert upon one another during embryonic growth. In the situation just described, it is

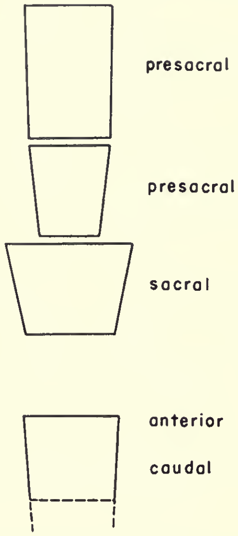


FIG. 86. Diagram representing the principal central proportions of the last two presacral vertebrae, the sacral, and an anterior caudal vertebra of *Procolpochelys grandaeva*.

possible that the centers of ossification of a spinal process and a neural plate, if they are in immediate spatial proximity, one beneath the other, will form a complete fusion. However, if two neural plate centers of ossification lie close to a spinal process, it may well be that the normal play of forces is sufficiently disturbed so that the result is not a fusion but a suture between the elements.

The last two presacral vertebrae and the first sacral vertebra of one individual are preserved (pl. 5). Since the sacral is relatively very large, these vertebrae probably belonged to one of the larger specimens (PU 16334 or PU 16335). There is, furthermore, an anterior caudal vertebra of even greater relative size (pl. 5), which may or may not belong to the same specimen. The size relationships between these elements (see fig. 86) differ notably from those of female specimens of Recent forms, which show a great sexual dimorphism as regards the length of the tail (see Carr, 1952, pp. 166, 358). We have no male individuals of any Recent cheloniid available

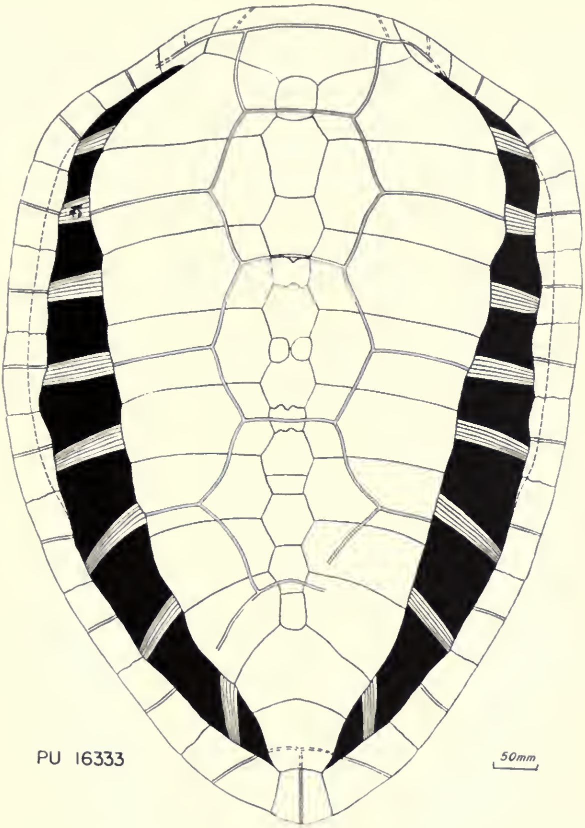


FIG. 87. *Procolpochelys grandaeva*, specimen PU 16333; reconstruction of the carapace.

for comparison, but it would seem reasonable to assume that the large sacral and caudal vertebrae of *Procolpochelys* are those of a male individual. Aside from differences in the relative size, the vertebrae of *Procolpochelys* (pl. 5) compare very well with those of female specimens of *Caretta*.

THE PHYLOGENETIC RELATIONSHIPS OF PROCOLPOCHELYS

The morphology of *Procolpochelys*, as described above, along with that of another Miocene cheloniid ("*Euclastes*" *melii* Misuri, 1910) shows a peculiarity indicative of a closer phylogenetic relationship with some of the Recent cheloniid sea turtles.

In another paper on fossil cheloniids, it became necessary to discuss the relationships among the Recent forms as they appear in the light of comparative-anatomical and paleontological evidence. The study (Zangerl, in press) led to the following conclusions:

(*a*) The very similar specialization of the limb skeletons in the four living cheloniid genera differs notably from that of the well-

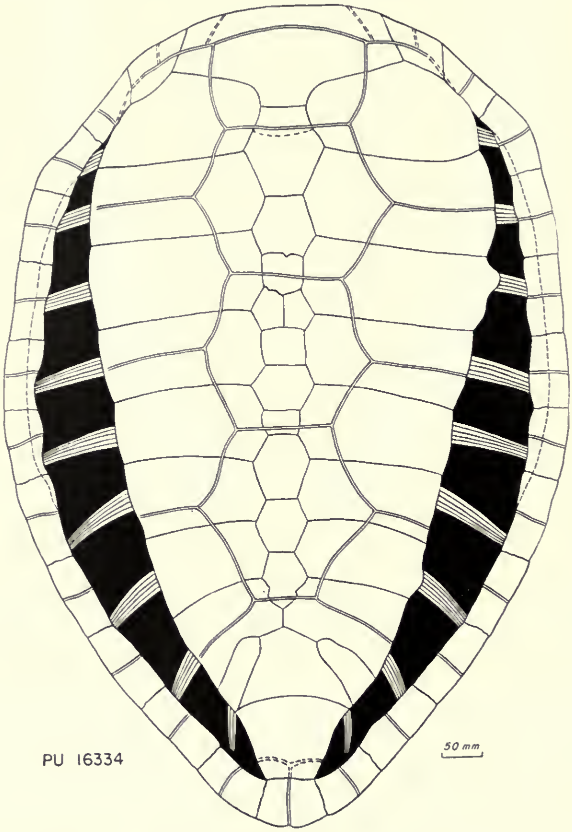


FIG. 88. *Procolpochelys grandaeva*, specimen PU 16334; reconstruction of the carapace.

known limbs of such Oligocene forms as *Glarichelys knorri* (Gray) and "*Chelonia*" *gwinneri* Wegner (1918) and such evidence as is afforded by the structure of humerus and femur of many other early cheloniids. Since highly differentiated, functionally successful

types of flipper and steering paddle construction are found in forms other than the Recent cheloniids (earlier cheloniids, Dermochelyidae, Protostegidae, Toxochelyidae, Desmatochelyidae), the striking similarity of these organs in the living forms is very probably due to close genetic relationship, rather than to convergence. Accordingly, the four Recent genera were included in the subfamily Cheloniinae.

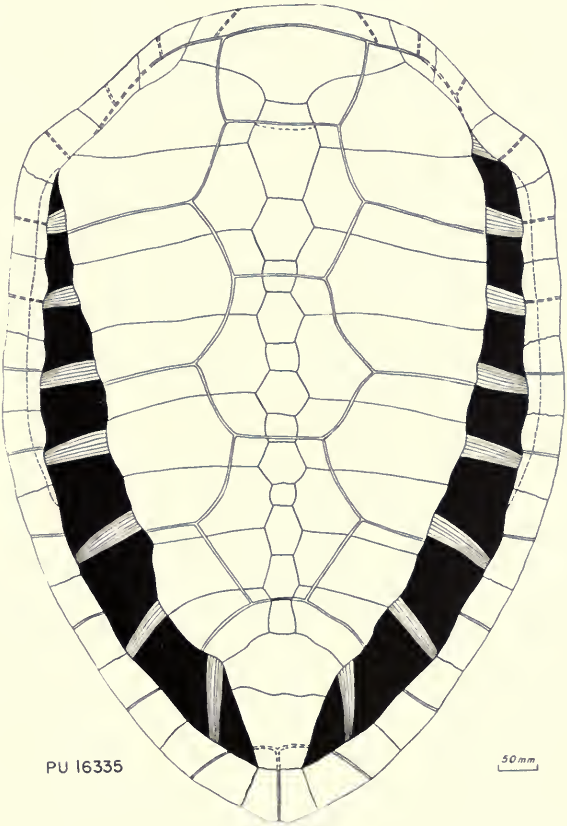


FIG. 89. *Procolpochelys grandaeva*, specimen PU 16335; reconstruction of the carapace.

(*b*) Within the subfamily, two groups were recognized and distinguished as follows:

1. Tribus Carettini: *Caretta*, *Lepidochelys*, +*Procolpochelys* (Miocene), +*"Euclastes" melii* (Miocene).

2. Tribus Chelonini: *Chelonia, Eretmochelys, +Chelonia sismondai* (Pliocene), *+Chelonia girundica* (Miocene).

The recognition of the two above groups among the Recent cheloniine turtles is not a novel proposal, though it is by no means universally accepted by herpetologists. The discussion of this matter calls for the examination of a questionable procedure used by many systematic zoologists, and the review of a controversial subject that may be described as the variation in the shell mosaic of the Carettini. These topics had to be touched upon in the paper cited (Zangerl, in press) but a fuller presentation of the matter was reserved for the present consideration of the phylogenetic ties of *Procolpochelys*.

The question as to the phylogenetic relationships among the Recent cheloniid turtles has been the subject of a fairly extensive literature. To this date, a general agreement has not yet been achieved, probably because of the intrinsic difficulties involved. (One major difficulty is the fact that there are no large series of adult specimens in any collection.) An examination of the procedures employed by students of the subject reveals the use of methods of highly questionable value in the determination of evolutionary ties.

Although these methods differ slightly from author to author, they have one common denominator: the morphological features considered (called "characters") are not rated as to their comparative-anatomical value. In other words, "characters" typical only of a single species or genus are valued equally with "characters" typical of the whole family or even order. The most illustrative example of this kind of procedure is given by Carr (1942) in his discussion of the topic in question. He appraises the relationships among the living cheloniids with the aid of a "similarity-dissimilarity table" in which 25 "characters" are compared in the four genera. He concludes: "The basis for separating *Chelonia* and *Eretmochelys* on the one hand from *Lepidochelys* and *Caretta* on the other is weak, being supported by a relatively small number of characters (four in the table) which are for the most part involved in a possibly independent reduction of the number of dorsal scutes in the former pair. Since scute number is generally subject to considerable variation, and is apparently a much less fundamental character than the osteological features, in which *Chelonia* and *Eretmochelys* diverge markedly, it seems likely that the points of agreement between the two forms should be attributed to parallelism. The elongated cora-

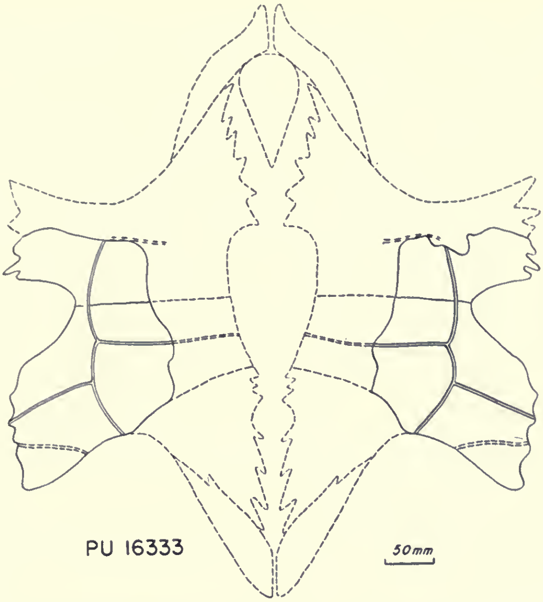


FIG. 90. *Procolpochelys grandaeva*, specimen PU 16333; reconstruction of the plastron.

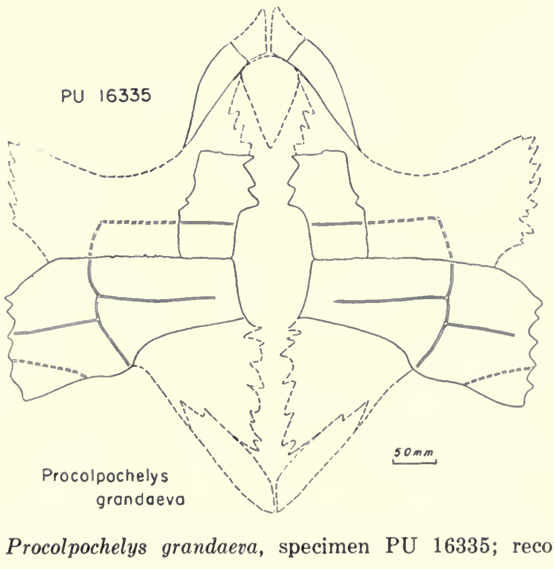


FIG. 91. *Procolpochelys grandaeva*, specimen PU 16335; reconstruction of the plastron.

coids of these two genera are associated with the fundamental adaptation of increased speed in swimming, and may also represent purely fortuitous agreement.

"If subdivision of the chelonioids is to be made, what appears to me as by far the most acceptable arrangement would restrict the Cheloniidae to the single genus, *Chelonia*, and place *Eretmochelys* in the Carettidae with *Lepidochelys* and *Caretta*. No fewer than fifteen characters supporting this disposition may be found in the table. On the other hand, there are certain striking similarities between the skulls of *Chelonia* and *Caretta* and between those of *Lepidochelys* and *Eretmochelys*. Moreover, the argument for monotypic family designation for each of the genera is not altogether unreasonable. Thus, until examination of large series of skeletons of each species has determined the relative constancy of the osteological characters involved, it would appear preferable to recognize only one family for all the marine Thecophora."

The difficulty in Carr's analysis lies in his failure to appraise the "characters" of his table as to their comparative-anatomical value.

Morphologists have long recognized as an axiomatic truth in their science that a given anatomical condition is of little (*erkenntnistheoretic*) value in itself. It assumes meaning only if measured (=compared) with a homologous anatomical condition in another individual, species, genus, or higher category. Such comparison (if the data are adequate) permits the evaluation of morphological conditions in relative terms as "generalized" or "derived" (or "primitive" or "specialized"). Thus, a character A may be found in the great majority of the individuals of a single species only, whereas a character B may also be found in all other species of the genus, moreover in all the genera of the family, perhaps in the great majority of the families of the order. Characters A and B therefore represent vastly different morphological situations that cannot be tabulated together in a similarity-dissimilarity chart and treated as equal entities.

Carr's table (1942) includes for the most part cranial features correlated with differences in the over-all proportions of the skulls in the compared forms.[1]

[1] Moreover, several of these "characters" reflect the same proportional relationships or regional peculiarities between the compared skulls. For example (Carr, 1942), such "characters" as "frontal entering orbital rim" and "external openings of orbits visible in ventral aspect" are both correlated with the relative width of the interorbital bridge; "premaxillary pit bordered laterally by strong

A survey of fossil cheloniid skulls shows that the secondary undershelving of the palate, the relative length of the snout region with its consequent effects upon the proportions of the entire skull, and the relative ventral concavity of the pterygoids, in fact, all osteological "characters" mentioned by Carr, occur in various combinations and in different degrees of expression. In the present state of our admittedly incomplete knowledge, the osteological "characters" listed by Carr do not occur repeatedly in similar combinations; instead, each form seems to present its own set of feature combinations. We are thus led to interpret these conditions as specialized, being found only within small systematic units, for example, species or genera.

On the other hand, Carr's table includes such structural features as the pattern of the carapace plates and shields. In this case, the comparative-anatomical situation found in *Chelonia* and *Eretmochelys* differs markedly from that of *Caretta* and *Lepidochelys*. The carapace mosaic in the first pair of genera (fig. 95, *Chelonia*) consists of a medial series of plates, namely, a nuchal in front, followed by eight neurals, two suprapygals, and a pygal, flanked by eight costals and eleven peripheral plates on each side; the superimposed epidermal shield pattern consists medially of a cervical scale, followed by five vertebrals, and these are flanked on either side by four pleural shields and twelve marginal scales (fig. 95, *Chelonia*). This arrangement of carapace elements is not only the normal carapace pattern of *Chelonia* and *Eretmochelys* but is found in all fossil Cheloniidae (except for *Procolpochelys* and "*Euclastes*" *melii*, see below) and moreover is the typical normal pattern in all but a few families of the order. Beyond doubt this is a pattern of very wide distribution among turtles, reaching back in the history of the order to the Plesiochelyidae of the late Jurassic.

The pattern of *Caretta* and *Lepidochelys*, compared to the generalized condition in *Chelonia* and *Eretmochelys*, shows what has been described as a marked tendency toward fragmentation of the carapace mosaic (Zangerl, in press). Instead of eight neural plates, there may be more (as many as fifteen); instead of eleven peripherals on each side, there are twelve in all adult and subadult specimens known to us (see also Deraniyagala, 1939). There may be more than five vertebral shields (fig. 93, *Lepidochelys*) and there are at

ridges," "median alveolar tooth of lower jaw connected with terminal tooth by sharp ridge," and "inner surface of upper beak strongly ribbed vertically," "edge of lower beak deeply dentate" are pairs of features related to the corresponding upper and lower jaw relief.

least five (and up to eight) pleural scutes and the regular number of marginals is thirteen on either side (figs. 92, 93, *Caretta* and *Lepidochelys*). The individual variation in the numerical composition of the carapace mosaic is very great in adult and subadult specimens. Neither among Recent nor among any fossil turtles is there a

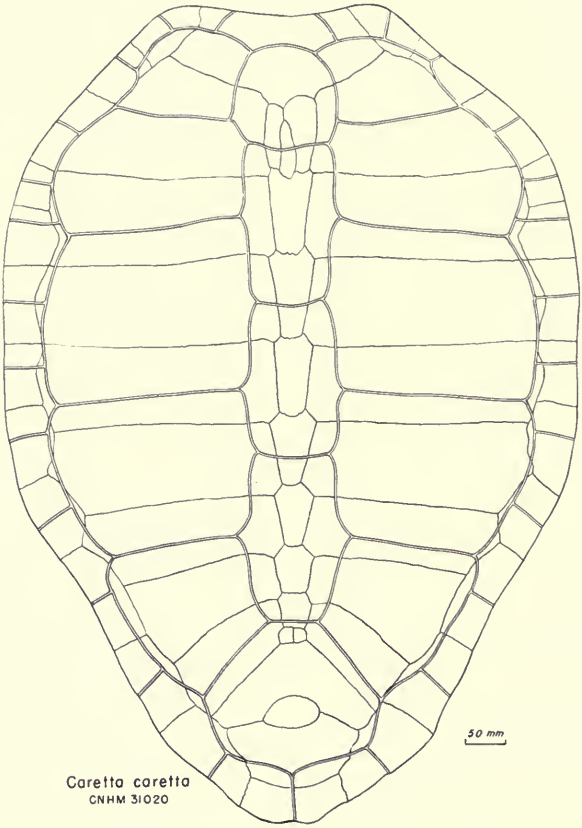


FIG. 92. *Caretta c. caretta*, CNHM 31020; carapace, dorsal view.

comparable condition of variation of the carapace pattern (in *Procolpochelys* and "*Euclastes*" *melii* the pattern is generalized, except for the fragmentation of the neural bones; see below). Compared to that of *Chelonia* and *Eretmochelys*, the carapace pattern of *Caretta* and *Lepidochelys* is thus a derived condition, found only in these two genera.

It may be noted that Carr (1942) and Deraniyagala (1939) expressed the extremely opposite opinion, namely, that a *reduction*

occurred in the shield number in *Chelonia* and *Eretmochelys* (see citation above). Neither comparative-anatomical nor paleontological evidence supports such a view, but it may be traced back to a study by Gadow (1899) on the individual variation of the carapace

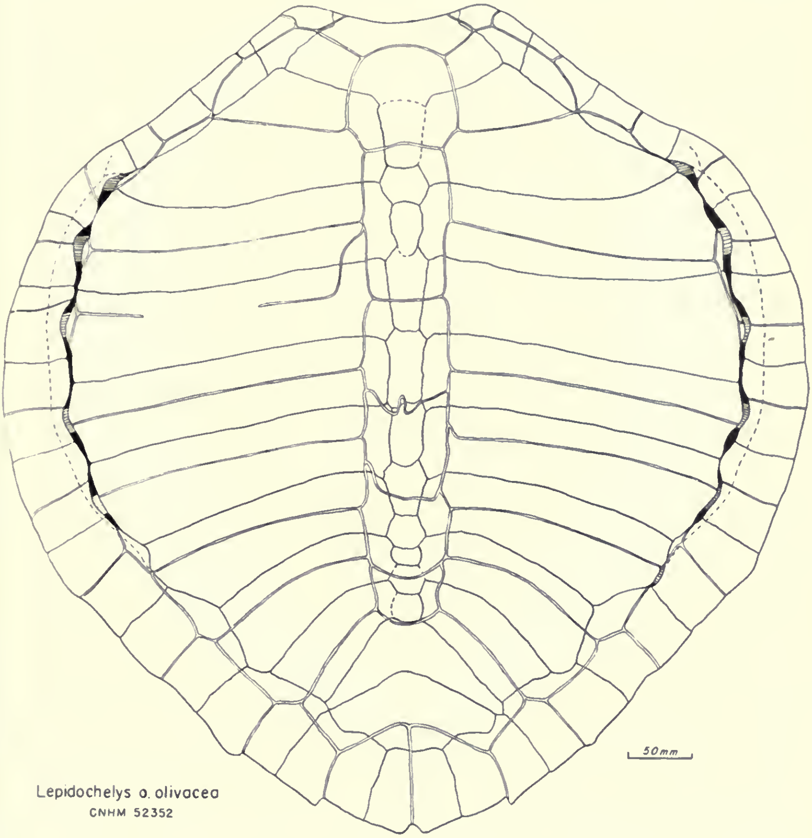


FIG. 93. *Lepidochelys o. olivacea*, CNHM no. 52352; carapace, dorsal view.

shield pattern in *Caretta caretta*, based largely on hatchling material. The supernumerary scutes were interpreted as atavisms in an effort to suggest the original congruence of bony plates and epidermal shields in the turtle armor. Based, in part at least, on similar evidence (large numbers of *Caretta* embryos and hatchlings), Coker (1910) strongly opposed Gadow's theory, with sound arguments, but he failed to suggest an alternative explanation for the obvious instability of the carapace pattern in *Caretta*.

Studies on pattern variation in turtles by Newman (1906, in *Chrysemys* and *Graptemys*) and Coker (1910, in *Malaclemys* and *Caretta*) and our own observations[1] furnish further evidence for the

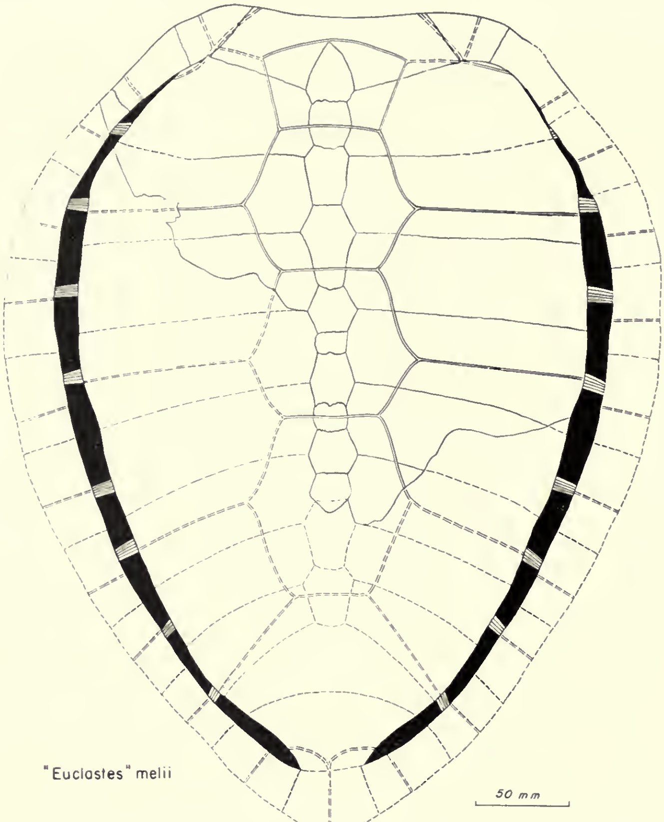


FIG. 94. "*Euclastes*" *melii;* reconstruction of the carapace, based on photographs by Misuri (1910).

interpretation of the instability of the carapace mosaic in the Carettini. Any such study reveals first of all an interesting fact, clearly recognized by Coker (1910) and formulated as follows: "From one point of view, the arrangement of scutes is exceptionally plastic or variable, while from another, the paleontological point of view, it is exceptionally persistent and fixed." The comparative anatomist, studying the shell pattern, is thus impressed with the relatively

[1] A renewed discussion of this matter, based on large numbers of specimens of many species, is in preparation.

great stability of this rather complex design. The herpetologist, accustomed to observing specific characters (rather than the shell pattern as a whole) in relatively large series of specimens, is more

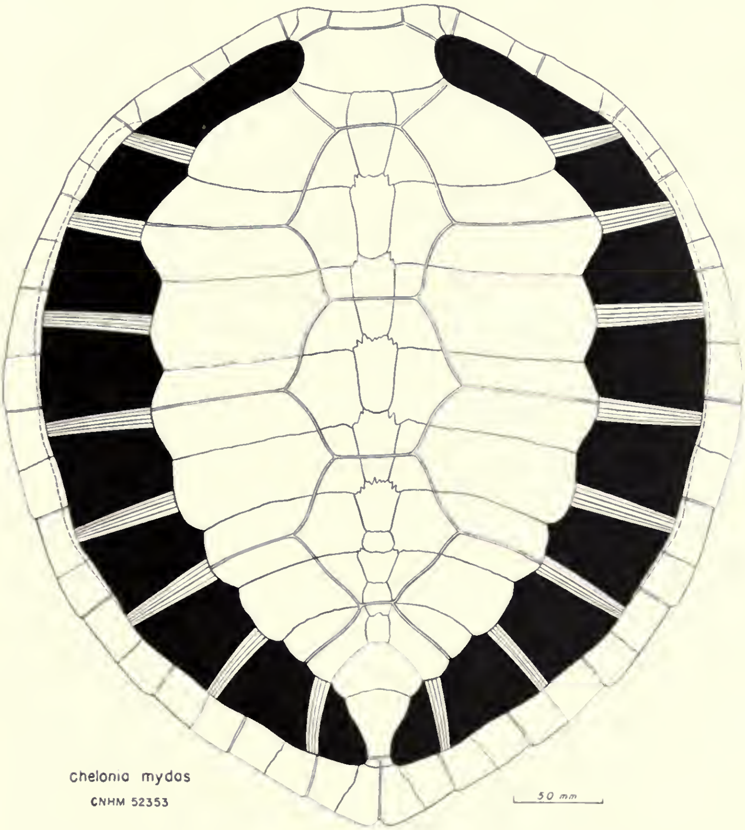


FIG. 95. *Chelonia mydas*, CNHM no. 52353; carapace, dorsal view.

conscious of individual variation and tends to overemphasize it. Even in relatively stable species, 30 per cent to 50 per cent of the individuals show some (but often very slight) deviation from the norm; yet there is no question as to the normal composition of the shell pattern. This fact should not be overlooked in the discussion of the carapace mosaic of *Caretta* and *Lepidochelys*.

Variation studies further suggest that not all of the deviations from the norm have the same causal relationships. Some variants would seem to be teratological conditions caused directly or in-

directly by environmental factors during early development in the egg (see Coker, 1910); as such they are purely somatic phenomena. But there are other, genetic deviations from the norm, and among these are variants that can be compared directly to elements of a phylogenetically older pattern (for example, the rather frequent occurrence of more than two inframarginal shields in emyid turtles), and others that seem to *foreshadow* evolutionary changes in the shell pattern. The latter situation appears to apply to the carapace mosaic of *Caretta* and *Lepidochelys* and requires further discussion.

Few students of Recent sea turtles have seen large series of adult and subadult specimens of *Caretta* and *Lepidochelys*, and all variational studies are largely based on embryos or hatchlings (see Gadow, 1899; Coker, 1910; Deraniyagala, 1939). Such material includes a large percentage of teratological individuals, most of which, in nature, apparently do not survive into adulthood. If one restricts the material to adult and subadult specimens, the number of individuals available is not sufficient for an adequate appraisal of variation; the specimens available to us and those illustrated in the literature permit, however, at least a tentative opinion as to the nature of the carapace mosaic in the two genera.

(*a*) The normal composition of the carapace mosaic in *Caretta* and *Lepidochelys*.

In spite of the great variability of the plate and shield pattern in these genera, it is possible to discern a norm, as follows: the bony theca consists of a median row—nuchal, eight neurals, two suprapygals, and pygal, flanked on either side by eight costals and twelve peripherals.[1] The shield pattern consists of one cervical and five vertebral shields, flanked by five (instead of four) pleural and thirteen (instead of twelve) marginal shields.[2]

This norm is subject to individual variation, as it is in other turtles, but there is, in addition, an obvious trend of variation in the direction of fragmentation, usually simple division of some of the elements of the normal pattern, namely, the neural plates, the vertebral and the pleural shields (fig. 93, *Lepidochelys*).

[1] Instead of eleven peripherals, as in *Chelonia*. There is an additional anterior peripheral, since the rib belonging to the first costal plate enters a pit in the fourth peripheral instead of in the third, as is usual in most turtles.

[2] The increase in the number of pleural scutes from four to five appears to be the result of an incorporation into the genotype of a factor for duplication of the first pleural of the typical cheloniid pattern. For the increase of the peripherals and marginals (from the typical P 11 and M 12 to P 12 and M 13) there is no equally simple explanation; circumstantial evidence suggests the addition to the genotype of a pair of peripherals and marginals anterior to the first pairs of these elements in the typical cheloniid scheme.

The neural plates may be divided lengthwise, as seen in a specimen of *Caretta* (fig. 92), or crosswise so that any or all neurals (never observed in N 1) are divided into anterior and posterior fragments (fig. 93, an extreme case illustrated by Deraniyagala, 1939, p. 149, fig. 60). This division of the neural plates has no effect on the number of costal plates.

Of the vertebral shields, numbers 2, 3, and 4 may be transversely divided (V 3 and 4 in the specimen illustrated in fig. 93, *Lepidochelys*) and the same applies to the pleural shields 3 to 5. In an extreme case, there may thus be eight instead of the normal five pleurals (fig. 93, left side). Vertebral shields may be duplicated independently from the pleural shields and vice versa, but if a pleural scute is divided and the corresponding vertebral shield is not, then the pleural division is often (though not always) incomplete, starting medially from a point, as in the third left pleural (fig. 93, *Lepidochelys*), which is only partially divided. In an extreme condition of this sort, illustrated by Deraniyagala (1939, p. 134, fig. 47), the alternate pleurals are pointed medially and the vertebral shields are normal in number.

In summary, it may be stated that the norm of the carapace pattern of *Caretta* and *Lepidochelys* shows, besides the usual variation also seen in other turtles, a definite trend toward fragmentation of the neural plate series, the vertebral and the pleural shields.

(*b*) Differences in the variation trends of the carapace mosaic between *Caretta* and *Lepidochelys*.

The following observations need confirmation, since the available number of adult and subadult specimens in each genus can hardly be considered statistically acceptable. The present material suggests that the carapace pattern of *Caretta* is more stable than that of *Lepidochelys* as regards the trend toward fragmentation of neurals, vertebrals, and pleurals. In the neural series, *Caretta* and *Lepidochelys* may possibly exhibit different trends. In *Caretta*, transverse fragmentation of neural elements was not observed (except in the area immediately anterior to the sacrum, which is very unstable in all turtles), and, particularly in the Pacific subspecies, there is a tendency toward reduction of the neurals (Deraniyagala, 1933, 1936, 1939). Of the four large specimens of the Atlantic loggerhead in our collection, two have a normal neural series, the third (fig. 92) shows fragmentation and the fourth indications of a mild reduction (neurals 6 and 7 are not in contact; the costal plates meet between them in the midline). Reduction of the neural series is not known in

Lepidochelys; here there is much fragmentation, usually in such a manner that each primary neural is transversely divided into two plates. Division of a neural plate into three parts, as in *Procolpochelys* (fig. 87), occurs rarely in *Lepidochelys* (see Deraniyagala, 1939, p. 151, fig. 62).

Regarding the fragmentation of the vertebral and pleural shields, *Caretta* appears to be much more stable than *Lepidochelys.* All

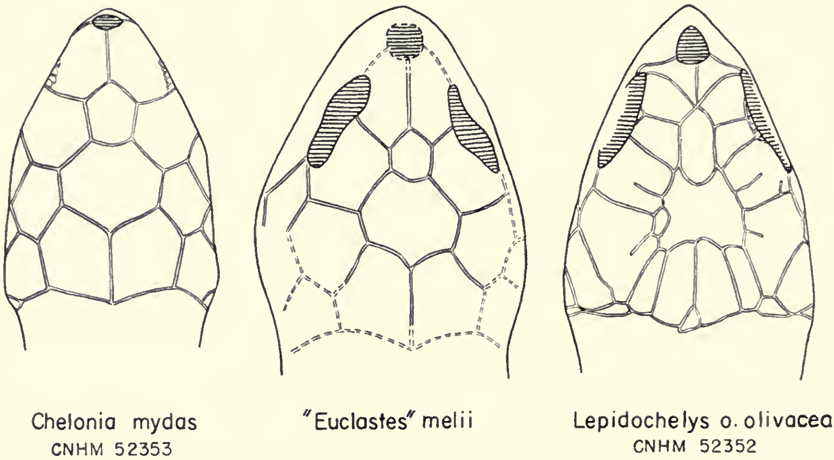


FIG. 96. Dorsal views of the head shields in *Chelonia mydas,* CNHM no. 52353, "*Euclastes*" *melii* (from Misuri, 1910), and *Lepidochelys o. olivacea,* CNHM no. 52352.

four specimens in our collection conform to the norm (see above) and so do those illustrated by Deraniyagala (1933, 1936, 1939), except in one case where there appears to be an extra scute anterior to the cervical (1933, pl. 5). A specimen figured by Carr (1942, pl. 1) has the fifth pleural divided on both sides.

In the discussion above, only the variation trends in the carapace mosaic of the Carettini were considered, but the tendency toward fragmentation is also evident in the pattern of the scales of the dorsal side of the head. In all cheloniid turtles, except the Recent Carettini, the dorsal surface of the head is covered with only a few shields (see fig. 96). In *Caretta,* and even more so in *Lepidochelys,* the shields of the typical pattern appear secondarily subdivided into a large but variable number of small scales (fig. 96).

The description of the shell of *Procolpochelys grandaeva* (above) revealed in the carapace a differentiation of the neural series similar to that found in the Recent *Lepidochelys olivacea.* The number of

peripheral bones and the shield pattern are entirely normal, that is, they conform to those of all fossil Cheloniidae and the Recent genera *Chelonia* and *Eretmochelys*. Another Miocene form, "*Euclastes*" *melii* Misuri (fig. 94), corresponds with *Procolpochelys* inasmuch as the neural series is similarly fragmented, while the rest of the carapace mosaic is normal. In this form, the skull is known (fig. 96) and the scale pattern on its dorsal side likewise corresponds to that of the typical cheloniid condition. *Procolpochelys* and "*Euclastes*" *melii* are thus forms that deviate from the typical cheloniid pattern only in the fragmentation of the neural plates, a condition also found in the Recent *Lepidochelys*. *Procolpochelys* has another morphological feature in common with the Recent Carettini, namely, the generalized shape of the plastron.

The shape of the plastron is quite characteristic in different families of sea turtles, in spite of the fact that it is correlated with the over-all outline of the shell (circular, oval, or elongated-cordiform). As set forth before (Zangerl, 1953 and in press), the primitive bridge index[1] in the Cheloniidae is about 55 and reaches, in the specialized genera, about 110. The increase in the bridge index is partially correlated with the relative elongation of the carapace, but it is moreover a peculiar feature of the Cheloniidae.[2] We do not know the plastra of many primitive fossil cheloniid turtles, but there is at least one form of late Cretaceous age, *Catapleura arkansas*, with a bridge index of 72. The relatively generalized Oligocene forms "*Chelonia*" *gwinneri* and *Glarichelys knorri* have plastral indices of about 65 and 69.4 respectively. Among the Recent sea turtles, the Carettini range from about 55 to 80, the Chelonini from 80 to 100 (see table, Zangerl, in press).

In *Lepidochelys*, a coastal form (Carr, 1942), the plastron is quite primitive and thus resembles that of the Toxochelyidae with its long hyo-hypoplastral suture and correlated absence of large central and lateral fontanelles. *Caretta*, a more elongated, advanced form (in the sense of marine specialization), likewise has a primitive plastron with a bridge index ranging slightly higher (observed values 61–78) than in *Lepidochelys* (observed values 55–67).

The plastral index can only be determined approximately in *Procolpochelys*. Assuming the hyoplastron to be somewhat narrower

[1] The shortest distance between axillary and inguinal notches × 100/half the width of the plastron.

[2] In the Toxochelyidae, for example (Zangerl, 1953), the primitive bridge index lies below 50 (in some of the genera it is as low as 35); in the elongated, pelagic genera, however, it does not exceed 60.

than the hypoplastron (as is the usual situation in cheloniid turtles), and by reconstructing the plastral fragments relative to the width of the carapace (see reconstructions, figs. 90, 91), the bridge index would lie somewhere between 70 and 85. In view of the fact that *Procolpochelys* is a pelagic form with elongated, fontanellized carapace, its plastron, with the long hyo-hypoplastral suture, shows unmistakably primitive proportions.

In the foregoing discussion of the fragmentation of the carapace mosaic in the Recent Carettini, we have set forth reasons suggesting the specialized nature of this phenomenon; the evidence strongly indicates that the evolution of the carapace pattern from the typical cheloniid condition to a new norm and the variational trend toward fragmentation of the neural plates and the vertebral and pleural shields, are rather recent occurrences in the history of the tribus Carettini. *Procolpochelys* and "*Euclastes*" *melii* document the beginning instability of the carapace mosaic (in the neural series).

The evidence presented strongly suggests a closer phylogenetic relationship between *Procolpochelys* and "*Euclastes*" *melii* on the one hand, and the Recent Carettini on the other. *Procolpochelys*, however, is very probably not directly ancestral to the living genera, having acquired a higher degree of pelagic specialization than the living Carettini. "*Euclastes*" *melii* (figs. 94 and 96) is probably less specialized than *Procolpochelys*. The unusual preneural plate, excavating the posterior border of the nuchal, may well be an individual variant in an unstable neural series.

Interpretation of the early history of the cheloniine sea turtles from the presently available evidence permits the following reconstruction of the sequence of events: During late Oligocene or early Miocene time, a group of cheloniid sea turtles evolved the type of limb skeleton typical of that of the Recent genera, forming the subfamily Cheloniinae (Zangerl, in press). The early forms had primitive plastra (see above) and fully ossified dorsal shells in the adult condition. The carapace mosaic and the epidermal shield on the dorsal side of the head were of typical cheloniid design.

One section of these early cheloniine turtles evolved specializations for a pelagic life—elongation of the shell, fontanellization of the carapace, extensive fontanellization of the plastron, and elongation of the plastron, resulting in a marked increase of the bridge index. In Miocene time, this group is represented by *Chelonia girundica*, in the Pliocene by *Chelonia sismondai*, and among the

Recent cheloniids by *Chelonia mydas* and *Eretmochelys imbricata;* this is the tribus Chelonini (Zangerl, in press).

Another section of the early Cheloniinae retained primitive plastral proportions (low bridge index) and, except for *Procolpochelys,* fully ossified dorsal shells in the adult state. But the carapace mosaic became unstable. At first this instability manifested itself in the fragmentation of the neural plates only, and one such representative, *Procolpochelys grandaeva* of Miocene age, became highly pelagic; another, "*Euclastes*" *melii,* was very probably a coastal form. These two forms represent early side lines of the tribus Carettini (Zangerl, in press). In the main line, the variational trend toward fragmentation of the carapace mosaic and the dorsal head shields affected especially the peripheral plates, the pleural shields, and the marginal scutes, as well as the head scales. Some of the variants became incorporated into the genotype and thus a new norm was evolved (see above).

In one group, the new norm became fairly stable (individual variation in adults probably not very much greater than that of most other species of turtles), and the group underwent moderate pelagic adaptation. This line is represented by the Recent genus *Caretta.* The most interesting variational peculiarity is the trend toward reduction of the neural series, probably more evident in the Pacific than in the Atlantic subspecies (Deraniyagala, 1936, 1939).

In another group the new norm remained, or has recently become, unstable. The trend toward fragmentation continues, affecting the vertebral and the pleural shields, the head scales (see above), and the neural plates, much as in *Procolpochelys* and "*Euclastes*" *melii.* This line is represented by the living genus *Lepidochelys,* a coastal form (Carr, 1942) of very great interest, since it is, so to speak, in statu nascendi of evolving a yet more highly fragmented carapace pattern.

SUMMARY

1. The Miocene sea turtle *Procolpochelys grandaeva* (Leidy) from the Atlantic seaboard of North America, hitherto known only from fragments, is redescribed from the prepared Princeton University material.

2. The material consists now of large portions of three shells and a few vertebrae.

3. *Procolpochelys grandaeva* is a large, elongated, marine turtle, with advanced features of pelagic specialization. Both carapace

and plastron show extensive fontanellization in the adult. The most remarkable feature of the carapace is the fragmentation of the neurals into two or three components each, much as in the Recent ridley (*Lepidochelys olivacea*).

4. The significance of the morphology of *Procolpochelys* (and a related Oligocene form, *"Euclastes" melii*) in the phylogeny of the four living genera of cheloniid sea turtles is discussed in detail.

5. The fallacies involved in such frequently employed methods as "similarity-dissimilarity" charts for the determination of phyletic ties are discussed in connection with the question of relationship among the four living genera of cheloniid sea turtles.

6. The evolution of the Carettini (*Lepidochelys* and *Caretta*) from the early Cheloniinae involved the fragmentation of the bony shell pattern and epidermal shield mosaic of the carapace and head. In *Procolpochelys* and *"Euclastes" melii*, this process finds an early expression in the division of the neural bones, the remainder of the pattern being normal.

7. The Carettini (*Procolpochelys, "Euclastes" melii, Lepidochelys,* and *Caretta*), while specialized as regards the fragmentation of the shell mosaic, are relatively primitive in the differentiation of the plastron (see p. 377).

8. The history of the turtles of the subfamily Cheloniinae probably dates back to late Oligocene or early Miocene time. The early stock were forms with primitive plastral proportions and the standard set of carapace bones and shields and a small number of head shields. They were probably inhabitants of near-shore waters.

In the course of subsequent evolution, the Chelonini acquired features of pelagic specialization without alteration of the fundamental morphology. In the Carettini, the plastron remained generalized. However, the shell plates and shields and the scales of the head show a progressive dissolution of the standard cheloniid pattern through fragmentation of its elements.

REFERENCES

CARR, A.

1942. Notes on sea turtles. Proc. New England Zool. Club, **21**: 1–16, 5 pls.

1952. Handbook of turtles. The turtles of the United States, Canada and Baja California. xv+542 pp., 37 figs., 14 tables, 23 maps, 82 pls. Comstock Publ. Assoc., Cornell Univ. Press, Ithaca.

COKER, R. E.

1910. Diversity in the scutes of *Chelonia*. Jour. Morph., **21**: 1–75, 17 figs., 14 pls.

COPE, E. D.

1868–69. Cook's geology of New Jersey. 735 pp.

1870. Synopsis of the extinct Batrachia and Reptilia of North America. Trans. Amer. Phil. Soc., **14**: 123–168.

1875. Synopsis of the Vertebrata of the Miocene of Cumberland County, New Jersey. Proc. Amer. Phil. Soc., **14**: 361–364.

DERANIYAGALA, P. E. P.

1933. The loggerhead turtles (Carettidae) of Ceylon. Ceylon Jour. Sci., ser. B, **18**, pt. 1, pp. 61–72, 6 figs., pl. 5.

1936. A further comparative study of *Caretta gigas*. Ceylon Jour. Sci., ser. B, **19**, pt. 3, pp. 241–251, 4 figs.

1939. Tetrapod reptiles of Ceylon, vol. 1. Ceylon Jour. Sci., Colombo Mus. Nat. Hist. Ser., xv+412 pp., 137 figs., 24 pls.

GADOW, H.

1899. Orthogenetic variation in the shells of *Chelonia*. Willey's Zoological Results, Part III, pp. 207–222, 2 pls.

HAY, O. P.

1908. The fossil turtles of North America. Carnegie Inst. Wash. Publ., no. 75, 568 pp., 704 figs., 113 pls.

LEIDY, J.

1851. [Several fossils from the Green Sand of New Jersey.] Proc. Acad. Nat. Sci. Phila., **5**: 329.

1856. Notice of remains of extinct turtles of New Jersey collected by Prof. Cook. Proc. Acad. Nat. Sci. Phila., **8**: 303.

LYDEKKER, R.

1889. Catalogue of the fossil Reptilia and Amphibia in the British Museum (Nat. Hist.), III. Chelonia. viii+235 pp., 53 figs. London.

MISURI, A.

1910. Sopra un nuovo chelonio del calcare miocenico di Lecce. Palaeontogr. Ital., **16**: 119–136, pls. 14–15.

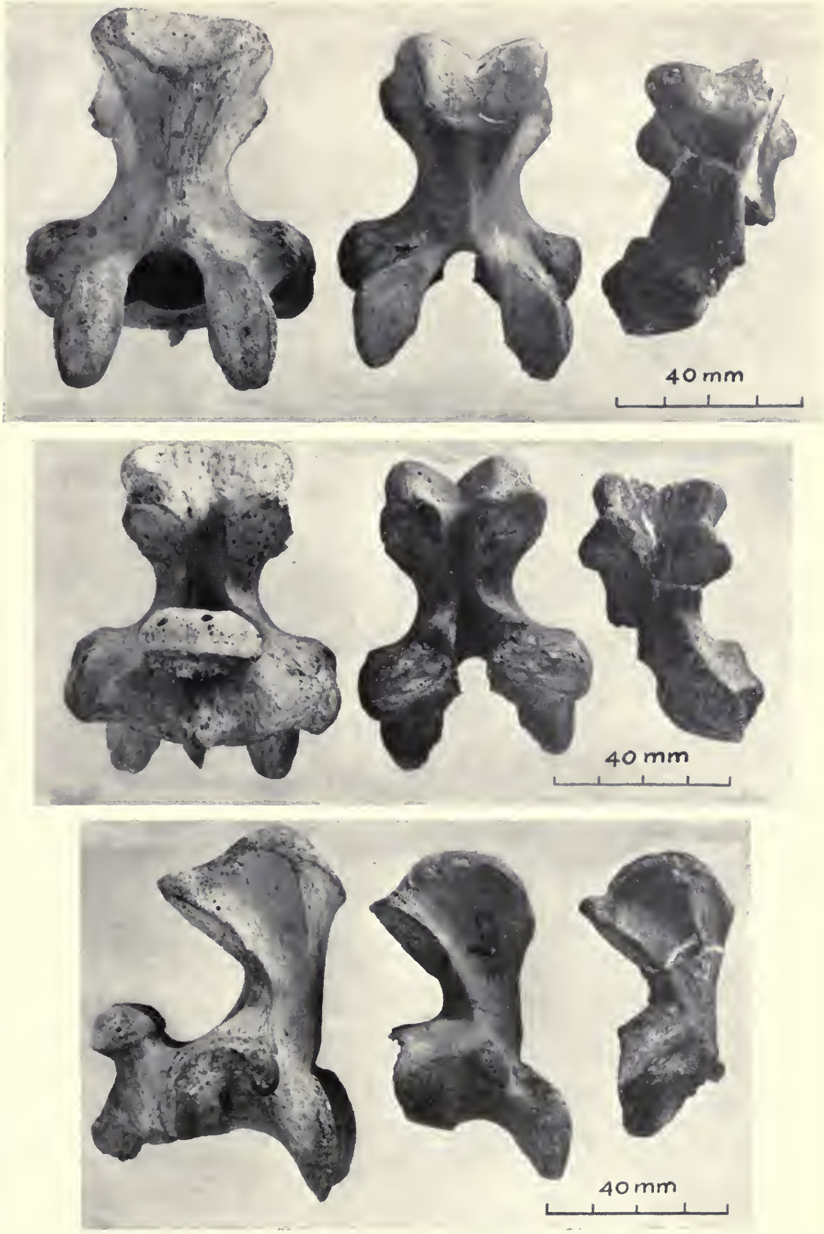
NEWMAN, H. H.

1906. The significance of scute and plate abnormalities in *Chelonia*. Biol. Bull., **10**: 68–114, fig. 58.

Wegner, T.
1918. *Chelonia gwinneri* Wegner aus dem Rupelton von Flörsheim a. M. Abh. Senck. Naturf. Ges., **36**: 359–372, 1 fig., pls. 28–30.

Zangerl, R.
1953. The vertebrate fauna of the Selma Formation of Alabama. Part IV: The turtles of the family Toxochelyidae. Fieldiana: Geology Mem., **3**, no. 4, pp. 135–277, figs. 60–124, pls. 9–29.

In press. Die Oligocaenen Meerschildkröten von Glarus. Abh. Schweiz. Pal. Ges.



Left to right: Eighth cervical vertebrae of *Chelonia mydas*, CNHM 22066; *Caretta c. caretta*, CNHM 31023; and *Procolpochelys grandaeva*, PU 16334. Top row, dorsal views; middle row, ventral views; bottom row, side views.

Procolpochelys grandaeva, PU 16334. Left to right: Two last presacral vertebrae, sacral vertebra, anterior caudal vertebra. Top row, dorsal views; middle row, side views; bottom row, ventral views.